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ON THE GUSTATORY ORGANS OF LEPUS AMERICANUS.

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ART. XXXIX—*On the Gustatory Organs of the American Hare, Lepus Americanus*; by FREDERICK TUCKERMAN.

General description of the tongue.

THE tongue of this rodent shows two well-marked divisions, a more or less flattened and expanded anterior portion, and a raised posterior part. The posterior division is the longer of the two by about one-fifth, the total length of the organ being 48^{mm}.

The anterior division is 13.5^{mm} in breadth, 5 to 8^{mm} in thickness, and is free from the floor of the mouth for 15^{mm}. The upper surface and lateral borders of this division are covered with small, closely set, cone-shaped papillæ, the apices of which are directed backward. The epithelium covering the papillæ is dense and imbricated, and in their upper half either partly or wholly cornified. They measure about 0.20^{mm} in height, and terminate in one or more minute spines. There is only the faintest trace of a mesial furrow on the papillate surface, but the organ is impressed transversely, corresponding to the palatal grooves. The apex is short, broad and obtuse. The under surface is smooth, and marked by a longitudinal median ridge extending from the tip of the tongue to the frænum. Papillæ of the fungiform type are not especially numerous. They are rather thinly distributed over the anterior dorsal surface, and the posterior division of the organ appears to be nearly devoid of them. They are however quite thickly set about the tip, particularly its inferior part, and they are also collected into a single line on each side of the tongue, from the apex to the anterior limits of the foliate organs.

The posterior division, which rises somewhat abruptly above the level of the preceding, is 11.5^{mm} in breadth and 8 to 12^{mm} in thickness. Anteriorly, the lateral margins of this division are stained a rusty-brown color. In some specimens this pigmentation of the epithelium involves nearly the whole of the anterior surface of the division. The upper surface is slightly convex, and, in front of the circumvallate area, is covered with closely-set mechanical papillæ, the points of which are directed backward. The extreme posterior region is traversed by a few inconspicuous ridges, in the furrows between which may be seen (with the aid of a lens) the minute orifices of the mucous ducts which open on the free surface in this region. The circumvallate papillæ are usually two in number. They are placed one on either side of the median line, 3.6^{mm} apart, and 10^{mm} from the base of the organ. Very rarely there are three papillæ of this type present. When this is the case, they are

arranged in a triangle, the apex of the triangle being directed backward toward the epiglottis. The foliate papillæ are situated obliquely on each side of the back of the organ, anterior to the glosso-palatine arch, their anterior extremity being directed downward and inward. Each papilla is about 5^{mm} long and 2.7^{mm} broad. As seen from above, they are small, oval-shaped elevations, and are marked transversely by a number of ridges or lamellæ with intervening furrows.

GUSTATORY STRUCTURES.

The circumvallate papillæ.—The general surface in front of these papillæ is covered, as already mentioned, with small conical papillæ. The immediate area around them, however, is nearly free from papillary elevations. When well developed the circumvallate papillæ measure 0.60^{mm} in diameter. Their summits are circular or slightly oval, and are more or less marked by verrucose elevations. Occasionally I have seen a fungiform papilla superposed upon one of this type. Each papilla is encircled by a narrow and rather shallow trench. Serous glands are abundant within the papillæ, and beneath and around them. Their ducts, which are numerous, open into the trench at its lower part. Mucous glands are also very plentiful in this region of the tongue, and their ducts have a greater diameter than those of the serous glands. They pass through the mucous membrane and open, somewhat obliquely, on the free lingual surface. In a horizontal section, two and a half millimeters square, I counted eighty ducts. The mucosa composing the body of the circumvallate papilla is cleft into three main portions, the central portion or lamella being much the largest, and overtopping the other two. In this particular the papilla bears a structural resemblance to the fold of the lateral organ, in which the mucosa is similarly arranged. The depressions between the lamellæ not infrequently extend to the base of the papilla, forming a deep and narrow furrow; usually, however, they are partially filled with epithelium. Covering the mucosa is a thin layer (0.03^{mm} in thickness) of stratified pavement epithelium. This layer is thicker above than at the sides, but the difference is only slight.

The taste-bulbs of this gustatory area occupy a somewhat exposed position. They are confined to the upper three fifths of the papillary wall instead of filling its lower and consequently more protected portion, as is the case in other Rodentia which I have investigated. They are also present in the corresponding region of the outer wall of the trench. The bulbs, to all appearance, are in contact by their edges and, in the papilla, are disposed in a zone of four to six tiers. Those embedded in the epithelium at the upper part of the outer

wall of the trench are arranged in a girdle of four or five tiers. From horizontal sections I estimated the average number of bulbs in a tier of the papilla at sixty. If we allow for five tiers, we shall have three hundred bulbs for each papilla. The average number of bulbs present in a tier of the outer wall of the trench appears to be about seventy-five, which, allowing for four tiers, would give three hundred bulbs for this region. The bulbs, as usual, vary in size and shape. The mean length is 0.051^{mm} and the mean breadth 0.033^{mm} . Most of the bulbs have a fairly well-developed neck, and in many of them the peripheral ends of the sensory cells project for some distance beyond the gustatory pore. The peripheral or supporting cells are elongated, slightly flattened structures, with an oval nucleus, containing several nucleoli, situated usually in their lower half. The outer end of the cells is more or less pointed, while their basal pole is generally slightly rounded, though it may be notched or even branched.* The sensory or taste-cells are fusiform, highly refractive elements, and consist of an elliptical-shaped nucleated enlargement, usually placed near the middle of the cell, and two processes. The peripheral process, broader than the central and quite straight, passes to the apex of the bulb, where it frequently terminates in a delicate hairlike projection. In other cells the apex of the peripheral process is truncated, but bears no cilium. The central process, more slender than the peripheral, and occasionally slightly varicose, sometimes divides below the nucleus into two or more branches, but more commonly it ends in a somewhat pointed extremity.

The circumvallate papilla is well supplied with nerves. Medullated and non-medullated fibers of the glosso-pharyngeus enter the papilla at its base, and ramify in all directions. In the mucosa directly beneath the bulb region, the finer branches form a delicate network. In chloride of gold preparations this subepithelial network is beautifully shown, the fibers of Remak and small ganglia, which are scattered through the membranous stroma, being stained deep violet or black. A portion of the terminal fibrils of the plexus enter the bulbs at their base, probably more than are represented by the sum of the taste-cells, while others pass between them and end freely in the epithelium or form an intra-epithelial network.

The papillæ foliatæ.—These papillæ measure 5^{mm} in length and 2.7^{mm} in breadth. Each papilla consists of thirteen or fourteen folds, most of which bear bulbs on their lateral area. The folds are separated by narrow furrows, slightly dilated at

* Hermann describes three kinds of supporting cells in the taste-bulb of the rabbit. First, the outer or "pillar cells," which constitute the true supporting element of the bulb. Second, the inner supporting cells, which resemble the "staff cells" of Schwalbe and heretofore supposed to be sensory in function; and, third, "basal cells" which he regards as compensating cells for the bulbs.

their base, and having an average depth of 0.30mm . The furrows are often partly filled with epithelium. The mucosa composing the body of each fold is divided into three quite symmetrical secondary folds or lamellæ. The primary or central lamella is taller and slightly broader than the two lateral, and at its upper part is frequently forked. The two secondary or lateral lamellæ contain the taste-bulbs. A thin stratum of stratified pavement epithelium is spread over the lamellæ, but is not sufficient to completely fill the depressions between them. Serous glands are abundant in this region, and their ducts, which are very numerous and occasionally of great length, usually open at the bottom of the furrows.

The taste-bulbs of this gustatory area are limited to the sides of the folds and, in the main, are restricted to their upper half. They traverse the epithelium more or less obliquely, and are so close as to be in actual contact. They are disposed four to seven tiers deep, the uppermost tier being on a level with the top of the lateral wall, while the lowest is about opposite the middle of the furrow. Each tier contains about thirty bulbs in its entire length. If we allow for five tiers, we shall have three hundred bulbs for each fold of the papilla. The bulbs have a clearly-defined neck, and, when well developed, are 0.056mm in length and 0.035mm in breadth.

The arrangement and distribution of the nerve-fibers in the folds of the foliate organ is very similar to that which exists in the circumvallate papilla. According to Drasch, who made the lateral gustatory organ of the rabbit and European hare a special study, there is beneath the basal membrane of the lateral lamella a plexus formed of medullated nerve-fibers. From this plexus, fibers, corresponding in number to the sum of the sensory cells, go directly to the bulbs. Other fibers, more numerous, pass between the bulbs to the epithelium situated above them. Many fibers, however, terminate in the membranous stroma. Below the bulb region, in the entire width of the lamella, is a connected stratum of ganglion cells which contribute to the multiplication of the fibers.

Other regions in which taste-bulbs occur, but which are not, strictly speaking, exclusively taste areas, are the fungiform papillæ and parts of the epiglottis. In the fungiform papillæ of *L. americanus* bulbs are but sparingly present, and only isolated ones were found in the epiglottis.